



A new and distinctive species of the hermit crab genus *Catapaguropsis* (Crustacea: Decapoda: Anomura: Paguridae) from the South China Sea

PATSY A. MCLAUGHLIN 1 & RAFAEL LEMAITRE 2

Shannon Point Marine Center, Western Washington University, 1900 Shannon Point Road, Anacortes, WA 98221-9081B, U.S.A. (hermit@fidalgo.net)

Smithsonian Institution, National Museum of Natural History, Department of Invertebrate Zoology, P.O. Box 37012, Washington, D. C. 20013-7012, U.S.A. (lemaitrr@si.edu)

Abstract

The diagnosis of the recently described hermit crab genus *Catapaguropsis* Lemaitre & McLaughlin, 2006 is emended to accommodate a second distinctive new species, *Catapaguropsis brucei* n. sp., which does not exhibit the sexual dimorphism described for the type species, *C. queenslandica* Lemaitre & McLaughlin, 2006. *Catapaguropsis brucei* n. sp. is characterized by the marked reduction, in both sexes, of the posterior portions of the pleons, uropods, and telsons that are encased by cnidarians. In addition to the description and illustrations, this new species is compared and contrasted with species of other pagurid genera that occupy atypical carcinoecia.

Key words: Crustacea, Decapoda, Paguridae, emended *Catapaguropsis*, new species, unique carcinoecia, South China Sea

Introduction

Catapaguropsis Lemaitre & McLaughlin, 2006 was proposed for two specimens that shared characters with Catapagurus A. Milne-Edwards, 1880 and Pteropagurus McLaughlin & Rahayu, 2006, but were clearly distinct from both. However, the male and female exhibited marked sexual dimorphism, with the female resembling species of Catapagurus and the male more similar to species of Pteropagurus. Additionally, they appeared to possibly occupy different habitats. No carcinoecia accompanied the specimens, so Lemaitre & McLaughlin (2006) could not be certain whether the marked reduction in the posterior portion of the male pleon, uropods and telson was habitat related or simply reflected abnormal development.

A pair of specimens recently found in the collections of the Muséum national d'Histoire naturelle, Paris, which are also assignable to *Catapaguropsis*, have provided the answer to the question of habitat influence, and at the same time shown that the dimorphism attributed to the genus is instead restricted, at least as far presently known, to the type species, *C. queenslandica* Lemaitre & McLaughlin, 2006. Consequently, the genus is emended to accommodate the new species, for which a detailed specific description and illustrations are provided, together with information on possible correlations between morphological adaptations and atypical carcinoecia.

The specimens used in this study are deposited the Muséum national d'Histoire naturelle, Paris (MNHN) with the catalog reference code Pg, and the Queensland Museum, Brisbane (QM) with the catalog reference code W. Terminology for the generic diagnosis and species' description follows that of Lemaitre & McLaughlin (2006) and McLaughlin & Rahayu (2006). It appears that shield width, rather than length, increases with growth in this genus; however, because of the contour of the shield, width cannot be as accurately measured.

Thus, shield length (sl), measured from the midpoint of the rostral lobe to the midpoint of the posterior margin of the shield is given as an approximation of animal size. The abbreviations FRV, cr., stn coll., and ovig. refer to Fisheries Research Vessel, cruise, station, collector, and ovigerous, respectively.

Taxonomy

Family Paguridae Latreille, 1802

Catapaguropsis Lemaitre & McLaughlin, 2006 (emended)

Catapaguropsis Lemaitre & McLaughlin, 2006: 58.

Diagnosis. Eleven pairs of biserial phyllobranchiate gills. Rostrum broadly subtriangular or reduced to broadly rounded lobe. Ocular peduncles with very slender penultimate segments, ultimate segments also slender proximately, but distally broadened, corneas prominently dilated; ocular acicles quite small, triangular. Antennal peduncles with supernumerary segmentation. Mandible with entirely calcified cutting edge except for small, corneous tooth at outer lower angle. Maxillule with external lobe of endopod rudimentary or vestigial. Maxilla with endopod exceeding distal margin of scaphognathite. First maxilliped with slender endopod exceeding distal margin of basial endite. Second maxilliped without distinguishing characters. Third maxilliped with crista dentata reduced or not, with accessory tooth. Sternite of third maxillipeds (thoracic somite IX of Pilgrim 1973) unarmed. Sternite of chelipeds (thoracic somite X) narrow, incompletely fused to larger sternite of second pereopods. Sternites of second and third pereopods (thoracic somites XI, XII) very broad, with distinct median concavities.

Chelipeds long, slender; right appreciably stouter, but not necessarily longer. Ambulatory legs sexually dimorphic or not; dactyls slender or somewhat blade-shaped. Fourth pereopods simple or semichelate, propodal rasp absent or consisting of single row of corneous scales; preungual process well developed. Fifth pereopods minutely chelate.

Males with short, stout right sexual tube directed toward exterior; very short left sexual tube or papilla; no paired or unpaired pleopods. Females with paired gonopores; no paired and modified first pleopods, unpaired biramous left pleopods 2–4, pleopod 5 absent. Pleon always reduced posteriorly in males, reduced or not in females. Symmetrical uropods reduced or not. Telson with transverse incisions weak or obsolete; posterior lobes separated by broad median concavity or by minute median cleft, unarmed or with few minute spinules.

Type species. Catapaguropsis queenslandica Lemaitre & McLaughlin, 2006, by original designation.

Distribution. Queensland, Australia and South China Sea; 296–388 m.

Remarks. The new species, described below, is clearly assignable to *Catapaguropsis* on the basis of male characters: sexual tube, absence of male pleopods, shape and reduction of the male pleon, symmetrical uropods, which are also markedly reduced in males, but differs from the type species in female characters. Of the similarities with the genus *Catapagurus* observable in the female of *Catapaguropsis queenslandica*, which include ambulatory legs with blade-shaped dactyls, ambulatory meri each with one or more subdistal spines on the dorsal surface, and the tendency for loss of the left fifth pleopod, only the latter loss is seen in the female of *C. brucei* n. sp.

In the male of *C. queenslandica*, as in both sexes of species of *Pteropagurus* McLaughlin & Rahayu, 2006, the third pereopods are markedly longer than the second. This dimorphism in *C. brucei* n. sp. is uncertain because only a single second right pereopod remains with the male paratype. Females of both *Catapaguropsis* species have ambulatory legs of generally equal length. The dimorphism in the fourth pereopods seen in *C. queenslandica* is not present in *C. brucei* n. sp.; both sexes have simple propodi, lacking propodal rasps. In *Catapaguropsis*, as in *Pteropagurus*, the sternite of the third pereopods is noticeably broadened. This

was thought to also be a dimorphic character in *Pteropagurus*; however, the posterior extension observed in males of *P. inermis* McLaughlin & Rahayu, 2006 and *P. spina* McLaughlin & Rahayu, 2006 was found to occur in both sexes in a third recently discovered species (McLaughlin, in press).

Certain inaccuracies in the original generic description of the mouthparts of C. queenslandica are corrected based on a reexamination of the female paratype and on the morphology of the new species. The maxillule was illustrated (Lemaitre & McLaughlin 2006: fig. 2B) as having a bilobed coxal endite; but reexamination of the maxillule has shown this condition to be an artifact. The coxal endite of the the maxillule of C. queenslandica and the new species is represented by a single lobe as is typical for paguroids in general. Similarly, the three-segmented exopods of the second and third maxillipeds (ibid.: fig. 2E, F) are artifacts; the exopods are two segmented as in most pagurids. The basis and ischium of the third maxilliped were illustrated (ibid.: fig. 2F) as being completely fused, and the crista dentata was described as lacking an accessory tooth. In the new species, when viewed externally, the basis and ischium similarly appeared to be completely fused, but internally, a suture line was visible. Reexamination has shown this also to be the case for C. queenslandica, indicating the basis and ischium must be considered incompletely fused. The crista dentata in the new species, when viewed externally, consisted of a row of translucent teeth decreasing in size anteriorly, but with one appreciably larger subdistal tooth. However, the internal view of the ischium showed that the crista dentata actually consisted of all small teeth distally and an adjacent subdistal large accessory tooth. The maxillule and second and third maxillipeds of C. queenslandica are herein illustrated accurately (Fig. 2a-c). The absence of an accessory tooth as a character that will distinguish Catapaguropsis from Catapagurus is not correct. Both genera have an accessory tooth on the crista dentata.

Catapaguropsis brucei n. sp. (Figs. 1, 2d,e, 3, 4)

Type material. South China Sea. *Holotype* female (sl = 2.4 mm), Cruise 4/65 stn 84, trawl 347, 12°02'N, 112°49'E, 366–388 m, 12 Mar 1965, coll. A.J. Bruce (MNHN Pg 7735). *Paratype*. Male (sl = 2.7 mm, missing second through fourth left and third right pereopods), same data as holotype (MNHN Pg 7736).

Description. Shield (Fig. 1a) somewhat vaulted, broader than long, moderately well calcified; anterior margin between rostral lobe and lateral projections concave; anterolateral margins sloping; posterior margin roundly truncate. Rostral lobe broadly rounded or roundly subtriangular, not produced beyond level of broadly rounded, unarmed lateral projections. Dorsal surface of shield with 2 subrostral, semiovate swellings and few sparse setae (not shown in Fig. 1a). Carapace lateral lobes narrow, not reaching 0.5 of shield in holotype, but reaching beyond in male paratype. Posterior carapace short, with broad median plate; cardiac sulci reaching to posterior margin. Branchiostegites membranous, unarmed.

Ocular peduncles very short, 0.6–0.7 length of shield, very slender penultimate segments visible dorsally, ultimate segments broadly expanded at bases of corneas; corneal diameter approximately equal to total peduncular length (including cornea). Ocular acicles very small, triangular, each terminally acute; separated basally by more than three times basal length of one acicle.

Antennular peduncles overreaching distal margins of corneas by approximately 0.5 length of penultimate peduncular segments; ultimate segment with several long setae at dorsodistal margin laterally; penultimate segment glabrous; basal segment with unarmed dorsolateral margin.

Antennal peduncles overreaching distal corneal margins by approximately 0.5 length of ultimate segments. Fifth and fourth segments unarmed; third segment with sparse tuft of setae on ventrodistal margin; second segment with dorsolateral distal angle produced, terminating in small spine, dorsomesial angle with small spine; first segment unarmed. Antennal acicle reaching beyond distal margin of fourth peduncular segment, slender, terminating in simple spine. Antennal flagella missing. Third maxilliped with tiny spinule on dorso-distal margin of merus.

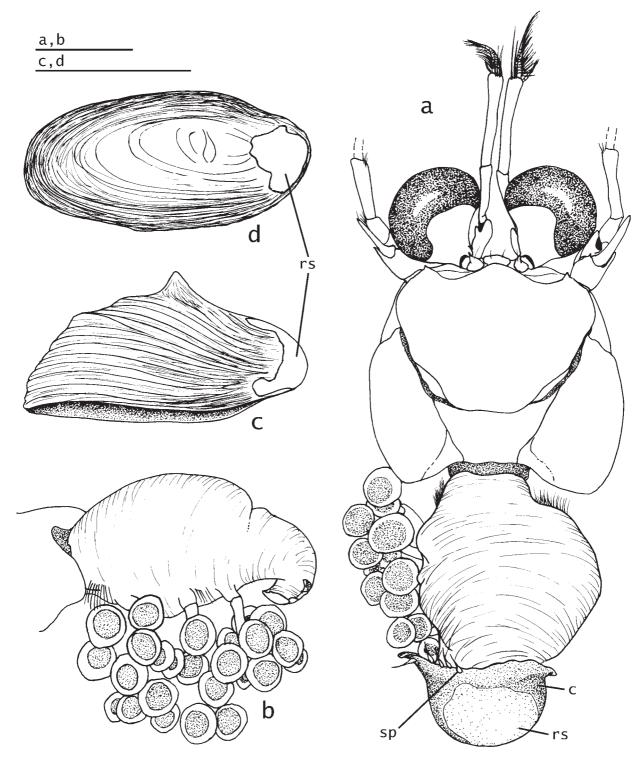


FIGURE 1. Catapaguropsis brucei n. sp., a, b, holotype ovigerous female (sl = 2.4 mm) (MNHN Pg 7735); c, d, carcinoecium of paratype male (sl = 2.7 mm) (MNHN Pg 7736). a, Shield, cephalic appendages, and pleon with eggs and cnidarian (actinian) covering uropods, telson, and part of pleon (dorsal view); b, pleon of same with carcinoecium removed, lateral view); c, d, same carcinoecium presumably produced by a cnidarian (actinian) in lateral (c) and dorsal (d) views. Abbreviations: c, cnidarian; sp, spermatophore; rs, remnants of shell. Scale equals 1 mm.

Chelipeds subequal in length in female, left exceeding right in distal extension in male by about length of dactyl; right appreciably stouter in both sexes; each lacking hiatus between dactyl and fixed finger. Right cheliped (Fig. 3a–c) with chela 2.6 (male) to 3.5 (female) as long as broad. Dactyl 0.3 (male) to 0.4 (female) length of palm; dorsomesial margin rounded, dorsal surface weakly convex, all surfaces unarmed but with

numerous scattered, moderately long setae ventrally; cutting edge serrate, with 2 low, broad, calcareous teeth, terminating in tiny corneous claw, slightly overlapped by fixed finger. Palm approximately equal to carpus in female, 0.4 longer than carpus in male, dorsomesial and dorsolateral margins rounded and unarmed, dorsal surface weakly convex, also unarmed, fixed finger similarly unarmed but ventral surfaces of both palm and fixed finger with numerous moderately long setae; cutting edge of fixed finger serrate, with 2 broad, low calcareous teeth and few much smaller distal calcareous teeth, terminating in tiny corneous claw. Carpus slightly shorter to slightly longer than merus; dorsomesial and dorsolateral margins each with row of irregularly-sized spines, largest on dorsomesial margins in both sexes, but spines of female largest; female also with 1 much larger spine at each dorsodistal angle; ventromesial and ventrolateral margins unarmed in female, male with few minute granules on ventrolateral margin. Merus laterally compressed; male with prominent spine on dorsodistal margin, row of low protuberances and few setae on dorsomesial margin, ventromesial and ventrolateral margins each with row of tiny spines; female with small spine on dorsodistal margin, other margins and surfaces unarmed, but with few setae dorsally. Ischium unarmed in both sexes.

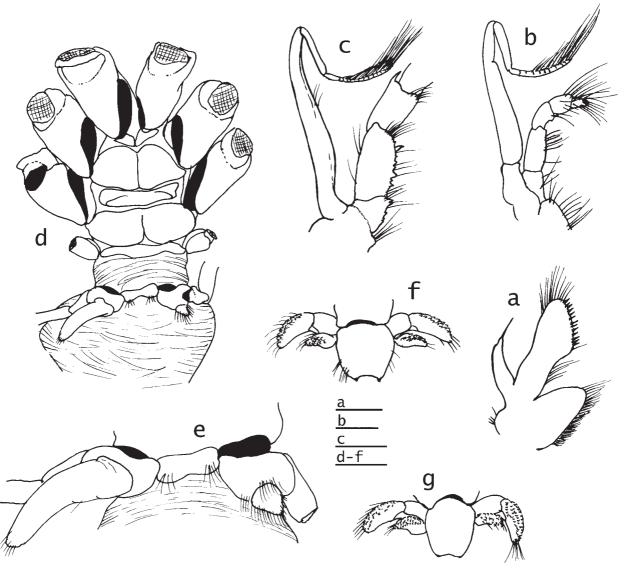


FIGURE 2. Catapaguropsis queenslandica Lemaitre & McLaughlin, 2006, a–c, paratype ovigerous female (sl = 1.9 mm) (QM W16589), left mouthparts (internal view): a, maxillule; b, second maxilliped; c, exopod, and basis to ischium of third maxilliped. Catapaguropsis brucei n. sp., d, e, g, paratype male (sl = 2.7 mm) (MNHN Pg 7736); f, holotype ovigerous female (sl = 2.4 mm) (MNHN Pg 7735): d, thoracic sternites (thoracic somites X–XIV), coxae of pereopods 1–5, and sexual tubes (ventral view); e, sternite of fifth pereopods (thoracic somite XIV), and coxae with sexual tubes (ventral view); f, g, telson and uropods. Scales equal 0.25 mm (a, b, d–f), and 0.5 mm (c).

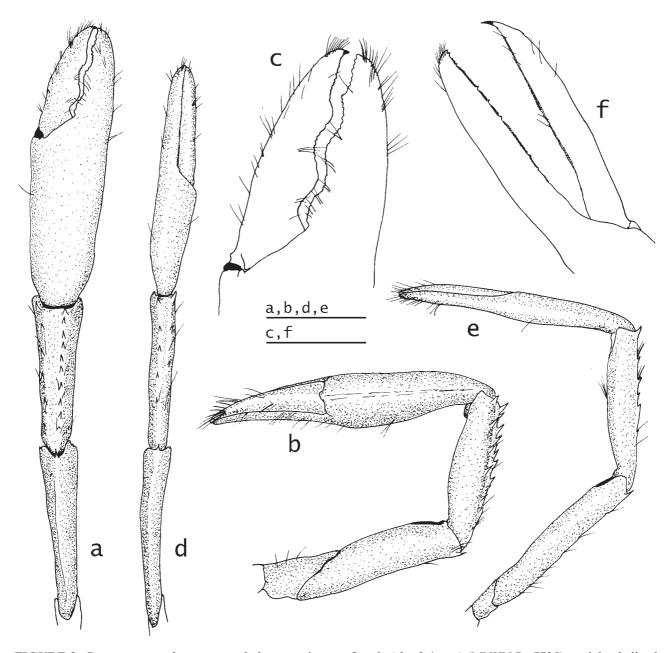


FIGURE 3. Catapaguropsis brucei n. sp., holotype ovigerous female (sl = 2.4 mm) (MNHN Pg 7735). a, right cheliped (dorsal view); b, same (mesial view); c, dactyl and fixed finger of same (dorsal view); d, left cheliped (dorsal view); e, same, lateral view); f, dactyl and fixed finger of same (dorsal view). Scales equal 1 mm (a, b, e, d), and 0.5 mm (c, f).

Left cheliped (Fig. 3d–f) long and very slender; left chela 5.7 (male) to 6.4 (female) as long as broad. Dactyl approximately 1.5 longer than palm; surfaces rounded and unarmed but with sparse, moderately short setae distally; cutting edge with row of tiny, calcareous teeth, terminating in minute corneous claw. Fixed finger similarly rounded and unarmed but with sparsely scattered setae; cutting edge with tiny calcareous teeth interspersed with minute corneous teeth, terminating in very small corneous claw and very sparse tuft of short setae. Palm with convex dorsal surface unarmed and glabrous; dorsomesial and dorsolateral margins rounded. Carpus and merus both noticeably longer than palm, but only slightly longer than dactyl. Carpus of female holotype with row of moderately widely-spaced small spines, 1 much larger spine on each dorsodistal angle, dorsolateral margin with row of smaller spines; male with even smaller spines on dorsomesial and dorsolateral margins, smallest laterally. Merus with very small dorsodistal spine in both sexes; surfaces unarmed; ventromesial and ventrolateral margins not delimited. Ischium unarmed.

Second and third pereopods (Fig. 4a, b) long, slender, terminating in slender corneous claws. Dactyls 0.7–0.8 length of propodi, not blade-shaped in either sex; dorsal and ventral surfaces each with row of moderately long setae. Propodi 2.2–2.3 length of carpi; dorsal surfaces each with dorsal row of very small spinulose protuberances, each with short, stiff bristle, ventral surfaces each with row of fine setae. Dorsal margins of carpi each with row of spinulose protuberances accompanied by short bristles, dorsodistal margins each with very small spine, smallest on third pereopods. Meri 2.4–2.5 length of carpi, each dorsally with minute protuberances accompanied by spiniform setae. Ischia unarmed. Fourth pereopods (Fig. 4c, d) simple, without propodal rasps; preungual processes nearly as long as dactylar claws; meri each with long setae dorsally and ventrally, densest dorsally. Fifth pereopods (Fig. 4e) minutely chelate. Sternites of second and third pereopods each with median concavity; anterior lobe of third subrectangular in both sexes.

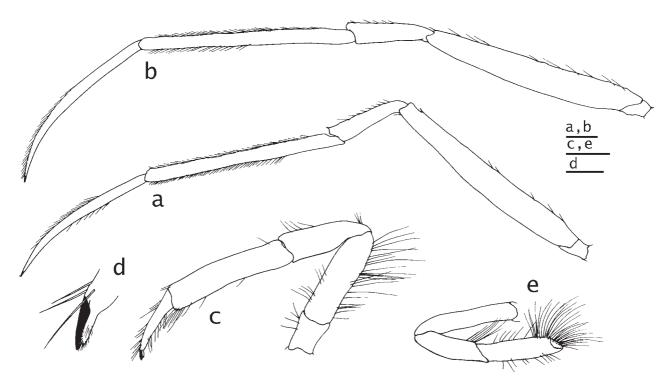


FIGURE 4. *Catapaguropsis brucei* n. sp., holotype ovigerous female (sl = 2.4 mm) (MNHN Pg 7735). a, left second pereopod (lateral view); b, left third pereopod (lateral view); c, left fourth pereopod (lateral view); d, claw (solid black) and preungual process of dactyl of same (lateral view); e, fifth pereopod (lateral view). Scales equal 1 mm (a, b), 0.5 mm (c, e), and 0.10 mm (d).

Male with coxae of fifth pereopods approximately equal, right with stout, short sexual tube appearing as posterior coxal extension (Fig. 2d, e) directed toward exterior; coxa of left with very short tube directed posteriorly; pleon bulbous anteriorly, markedly reduced posterior to position of pleopod 4; no paired or unpaired pleopods. Female with paired gonopores; without paired, modified first pleopods, pleon similarly bulbous anteriorly, reduced posterior to pleopod 4, left pleopods 2–4 well developed, biramous, no unpaired fifth pereopod; non-eyed eggs 0.5–0.6 mm diameter.

Uropods and telson (Fig. 2f, g) symmetrical in both sexes, markedly reduced. Telson with slight lateral incisions or indentations separating anterior and posterior portions; posterior lobes separated by minute median cleft; terminal margins horizontal, with 1 or 2 microscopic spinules.

Etymology. It is a pleasure to dedicate this species to its collector, the noted carcinologist, Dr. Alexander J. (Sandy) Bruce.

Color. Unknown.

Habitat. The carcinoecium (Fig. 1c, d) found with the male is a *Crepidula*-like chitinous pseudoshell with a small piece of calcified shell remaining posteriorly. Although no tissue was found with this carcinoecium, the chitinous portion is likely to have been produced by a cnidarian, probably an actinian. Chitinous pseudoshells are produced by a number of actinians and zoanthids that associate with various deep-water hermit crab species (e.g., Fautin Dunn *et al.* 1980; Lemaitre 1989, 2004). The carcinoecium was disassociated with the male when the specimen was examined, but its size suggests that it covered only the uropods and telson of the animal.

The female's carcinoecium, while still in place on the specimen (Fig. 1a), is slightly larger and consists of a cnidarian of unknown identity, probably an actinian (A.G. Collins, personal communication), covering a gastropod shell of the family Architectonicidae. Several spermatophores, presumably from a male of this new species, were found attached near the anterior margin of the carcinoecium, and several more were also attached on the interior wall of the carcinoecium (hidden from dorsal view, Fig. 1a) (C.C.Tudge, personal communication). No evidence of a pseudoshell was found with this carcinoecium, which covers only the uropods and telson.

Distribution. Known only from the type locality.

Variation. The marked sexual dimorphism apparent in *C. queenslandica* appears to be absent in *C. brucei*, although additional specimens may show that the male second and third pereopods are dissimilar in length as they are in the former species.

Remarks. Had *Catapaguropsis* not initially been proposed for the sexually dimorphic and similarly female characters of *C. queenslandica*, the relationship of *Catapaguropsis* to *Catapagurus* might not have been immediately recognizable. The only significant characters that *C. brucei* n. sp. shares with some species of *Catapagurus* are the short, stout ocular peduncles, elongate chelipeds and ambulatory legs, finely spinose carpi of the chelipeds, broad thoracic sternites 2 and 3, and the male right sexual tube, but none of these characters are mutually exclusive for the two genera. As indicated by Lemaitre & McLaughlin (2006), the shared male characters suggest a much closer relationship with *Pteropagurus*, despite differences in pleon reduction; however, neither are these characters mutually exclusive to those two genera.

As previously noted, the carcinoecia of *C. queenslandica* are not known. Lemaitre & McLaughlin (2006) speculated that they could differ for males and females because of the marked reduction of the posterior pleon, uropods and telson in the single known male of that species. That the reduction did not result from injury or abnormal development has been clearly shown by the similar reductions seen in both sexes of *C. brucei* n. sp. Nonetheless, it is uncertain whether the different carcinoecia occupied by the male and female of the latter species reflect actual selection differences or simply availability. Both carcinoecia protect only the posterior portions of the pleons, uropods and telsons (Fig. 1c, d). The relatively large clutch of developing eggs of the female of *C. brucei* n. sp. is completely exposed.

Discussion

Reduction in the size of the pleon is not unique to *Catapaguropsis*, but it is unquestionably different. In the family Paguridae, pleons also are reduced in *Alainopagurus* Lemaitre & McLaughlin, 1995, *Alainopaguroides* McLaughlin, 1997, *Porcellanopagurus* Filhol, 1885, *Solitariopagurus* Türkay, 1986, and *Ostraconotus* A. Milne-Edwards, 1880. Of these five genera, in all but *Ostraconotus*, reduction takes the form of a shortening and broadening of the pleon, giving it a globular appearance. In the latter genus, the pleonal segments all are reduced in length and width, resulting in an extremely short, narrow pleon. Pleonal reduction in *Catapaguropsis* differs in that marked reduction begins only at a level just posterior to the position of the fourth pleopod. These six genera share several characters that set them apart from other genera of the family, but whether these are indicative of phylogenetic relationships rather than phenotypic adaptations to specialized habitats

has not been investigated. Males of these genera lack all pleopods. Similarly, the uropods are symmetrical in both sexes and females have only unpaired pleopods 2-4. Males of all but *Porcellanopagurus* have a right sexual tube, although in some genera a pair of tubes may be present. Despite these possible shared apomorphies, all of the aforementioned genera are readily differentiated from one another. However, these genera have another attribute in common and that is that they do not utilize gastropod shells for protection. Alainopagurus, Alainopaguroides, Porcellanopagurus, and Solitariopagurus species, as far as is known, primarily carry halves of bivalve shells over their pleons (Komai & McLaughlin 2005). McLaughlin (1997), however, reported the one carcinoecium found with a specimen of Alainopaguroides lemaitrei McLaughlin, 1997 was a gastropod shell well-covered by an anemone. Lemaitre & McLaughlin (1995) suggested that two additional characters indicating similarities in habitats among Alainopagurus, Porcellanopagurus and Solitariopagurus were the hook-like dactyls of the fourth pereopods and the broadly rounded exopodal rasps of the uropods. Similar hook-like dactyls were also reported for Alainopaguroides andamanensis McLaughlin, 2002 by Komai & McLaughlin (2005), but not broadly rounded exopodal rasps for the uropods. In contrast, the dactyls of the fourth percopods of A. lemaitrei were illustrated as simple and the uropodal rasps elongate and moderately narrow (McLaughlin 1997: figs. 10k, 10f). Catapaguropsis brucei n. sp. and males of C. queenslandica have simple fourth pereopods, and reduced uropodal rasps.

The methods used by the genera of hermit crabs to secure bivalves in place appear to vary, although no detailed studies have been done. McLaughlin (2000) reported specimens of Porcellanopagurus filholi de Saint Laurent & McLaughlin, 2000 found with their telsons and the endopods of the uropods securely lodged in the umbos of their respective bivalve shells. It is presumed that the hook-like dactyls of the fourth pereopods grasped the shell margins. However, the majority of specimens of this same species from Sagami Bay, Japan recently examined by the first author occupied a variety of bivalves, including many that did not have well developed umbos. These carcinoecia seem to be held in place by the combined use of the telsons, spatulate rami of the uropods, and the posterior portions of the fleshy, bulbous pleons, perhaps at least in part aided by the hydrostatic pressure developed in the pleons (Chapple 1973). Despite these atypical carcinoecia, all provide protection for the membranous pleons and for the females' developing eggs. In species of Porcellanopagurus and Solitariopagurus, females carry their eggs dorsally, directly under the shell; the egg-carrying positions have not been recorded for species of Alainopagurus and Alainopaguroides, but it is presumed that they are carried on the left side of the pleon as in most pagurids. In contrast, Ostraconotus spatulipes A. Milne-Edwards, 1880 is described as using a cup-like small shell (Balss 1924: 763); the female's eggs are carried ventrally and protected from the substrate by the broad, spatulate propodi of the fourth pereopods that are flexed over the developing ova (A. Milne-Edwards & Bouvier 1983: pl. 12, fig. 2).

The spermatophores found attached to the carcinoecium of the female *Catapaguropsis brucei* n. sp. are intriguing, assuming that they were indeed transferred by a male of this new species. Their general shape is unlike any so far documented for any paguroid, and instead bear striking similarities to that described by Tudge & Jamieson (1996) for the porcellanid crab *Petrolisthes lamarckii* (Leach, 1820). Preliminary observations under light microscopy of the sperm cells in these spermatophores show that their overall morphology is similar to that described for sperm of *Solitariopagurus tuerkayi* McLaughlin, 1997 (Tudge 1995: 255, fig. 1G (as *Porcellanopagurus* sp.), Jamieson & Tudge 2000: 26, table 3). It is tempting to suggest that these two genera, as well as *Alainopagurus*, *Alainopaguroides*, and *Ostraconotus* might all share spermatozoal apomorphies as well. However, despite significant advances in documenting decapod sperm morphology (e.g., Jamieson & Tudge 2000), too few paguroids have been investigated so far to suggest any phylogenetic connections.

In their review of hermit crab biocoenoses, Williams & McDermott (2004) opened their report with the statement that hermit crabs are decaped crustaceans most of which have non-calcified pleons requiring protection from predation. These authors documented over 550 invertebrates from 16 phyla that were associated with 180 hermit crab species. Of these, the authors reported that approximately 100 were enidarians. The ben-

efits to the hermit crabs from symbionts such cnidarians, through extensions of shell apertures and predator protection, have been studied in detail, but with the emphasis on species associated with particular hermit crabs and their shells. However, at least some zoanthids either attach directly to the body of the hermit crab or dissolve the shell initially occupied by the crab (Boas 1926; Lemaitre 1998; Altes 2003). The latter condition appears to be the case for the male of *C. brucei* sp., whereas the shell of the female seems only to have an external cnidarian covering a shell. In *C. brucei* n. sp., the cnidarians do not protect the pleons, and that of the female does not appear to offer any protection for the eggs developing on the three left pleopods. Nor are there modifications of the fourth pereopods to afford cover. However, the protected, markedly reduced posterior portions of the pleon, uropods and telson, and the simple terminations of the fourth pereopods of this species and of males of *C. queenslandica* suggest that these animals may utilize supplemental cryptic covers, open posteriorly as well as anteriorly, for which the encasement of the telson and uropods by the cnidarians would provide the additional needed protection. An analogous condition is seen in species of *Xylopagurus* A. Milne-Edwards, 1880 that inhabit cylindrical pieces of wood, open at both ends and secured posteriorly by the well-calcified, operculate telson. Males of *Xylopagurus* lack unpaired pleopods 3–5 and females lack pleopod 5 (Lemaitre 1995).

Acknowledgements

The authors are indebted to Dr. Alain Crosnier, USM Taxonomie-Collections, Départment Systématique et Évolution, Muséum national d'Histoire naturelle, Paris, for making the material available for study. We acknowledge, with gratitude, Dr. Hajime Watabe, Ocean Policy Research Foundation, Tokyo, for the loan of several dozen specimens of *Porcellanopagurus filholi* from Sagami Bay; Dr. Allen G. Collins, National Marine Fisheries Service, Systematics Lab, Smithsonian Institution, Washington D.C., for comments on the cnidarian carcinoecia; and Dr. Christopher C. Tudge, American University, Washington D.C., for recognition of the spermatophores. Rose A. Gulledge assisted in the preparation of the illustrations. This is, in part, a scientific contribution from the Shannon Point Marine Center, Western Washington University.

References

- Altes, R.M.L. (2003). A preliminary review of zoanthid-hermit crab symbioses (Cnidaria; Zoantharia/Crustacea; Paguridea). *Zoologische Verhandlingen*, 345, 41–48.
- Balss, H. (1924). Über Anpassungen und Symbiose der Paguriden eine Zusammenfassende übersicht. Zeitschrift für Morphologie und Okologie der Tiere, 1, 752–792.
- Boas, J.E.V. (1926). Zur Kenntnis des Einsiedlerkrebses *Paguropsis* und seiner eigenartigen Behausung. *Konelige Danske Videnskabernes Selskabs Skrifter, Biologiske Meddelelser*, 5(7), 1–23.
- Chapple, W.D. (1973). Hydrostatic pressure changes in the abdomen of the hermit crab *Pagurus pollicarus* [sic] during movement. *Journal of Comparative Physiology*, 88, 399–412.
- Fautin Dunn, D., Devaney, D.M., & Roth, B. (1980). *Stylobates*: a shell-forming sea anemone (Coelenterata, Anthozoa, Actiniidae). *Pacific Science*, 34(4), 379–388.
- Filhol, H. (1885). Description d'un nouveau genre de Crustacés provenant de la Nouvelle-Zélande. *Bulletin de la Société Philomatique de Paris*, (7)9, 47–48.
- Komai, T. & McLaughlin, P.A (2005). New record and supplemental description of *Alainopaguroides andamanensis* McLaughlin (Decapoda: Anomura: Paguridae). *Crustacean Research*, 34, 53–64.
- Latreille, P.A. (1802). *Histoire naturelle, générale et particulère, des Crustacés et des Insectes*. F. Dufart, Paris, volume 3, 480 pp.
- Leach, W.E. (1820). Galatéadées. *In*: Cuvier, F.G. (ed.). *Dictionnaire des Sciences Naturelles &c. &c.* Vol. 18, Paris, pp. 49–56.
- Lemaitre, R. (1989). Revision of the genus *Parapagurus* (Anomura, Paguroidea, Parapaguridae), including redescriptions of the western Atlantic species. *Zoologische Verhandelingen*, 253, 1–106.

- Lemaitre, R. (1995). A review of the hermit crabs of the genus *Xylopagurus* A. Milne Edwards, 1880 (Crustacea: Decapoda: Paguridae), including descriptions of two new species. *Smithsonian Contributions to Zoology*, 570, 1–27.
- Lemaitre, R. (1998). Revisiting *Tylaspis anomala* Henderson, 1885 (Parapaguridae), with comments on its relationships and evolution. *Zoosystema*, 20(2), 289–305.
- Lemaitre, R. (2004). A worldwide review of hermit crab species of the genus *Sympagurus* Smith, 1883 (Crustacea: Decapoda: Parapaguridae). *In*: B. Marshall & B. Richer de Forges (eds), Tropical Deep–Sea Benthos, 23. *Mémoires du Muséum national d'Histoire naturelle*, 191, 85–149.
- Lemaitre, R. & McLaughlin, P. A. (1995). *Alainopagurus crosnieri* n. gen., n. sp. (Decapoda: Anomura: Paguridae) from the western Pacific. *Bulletin du Muséum national d'Histoire naturelle*, (4) 17A(3-4), 273–282.
- Lemaitre, R. & McLaughlin, P.A. (2006). A new genus and species of the hermit crab family Paguridae (Crustacea: Decapoda: Anomura: Paguroidea) from Australia. *Zootaxa*, 1297, 57–68.
- McLaughlin, P.A. (1997). Crustacea Decapoda: Hermit crabs of the family Paguridae from the KARUBAR cruise in Indonesia. *In*: A. Crosnier & P. Bouchet (eds), Résultats des Campagnes MUSORSTOM,16. *Mémoires du Muséum national d'Histoire naturelle*, 172, 433–572.
- McLaughlin, P.A. (2000). Crustacea: Decapoda: Species of *Porcellanopagurus* Filhol and *Solitariopagurus* Türkay (Paguridae), from the New Caledonia area, Vanautu, and the Marquesas: new records, new species. *In*: A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM, 21. *Mémoires du Muséum national d'Histoire naturelle*, 184, 389–414.
- McLaughlin, P.A. (2002). A review of the hermit crab (Decapoda: Anomura: Paguridea) fauna of southern Thailand, with particular emphasis on the Andaman Sea, and descriptions of three new species. pp. 385–460. *In:* N. Bruce, M. Berggren & S. Bussawarit (eds), Proceedings of the international workshop on the Crustacea in the Andaman Sea, Phuket Marine Biological Center 29 November–20 December, 1998. Phuket Marine Biological Center, Special Publication, 23(1–2), i–xii + 532 pp.
- McLaughlin, P.A. (in press). Hermit crabs from New Caledonia's Exclusive Economic Zone. Part I. A new species of *Pteropagurus* McLaughlin & Rahayu and a new genus and species of scaphopod dweller (Decapoda: Anomura: Paguroidea: Paguridae). *Zoosystema*
- McLaughlin, P.A. & Rahayu, D.L. (2006). A new genus with two new species of hermit crabs (Crustacea, Decapoda, Paguroidea, Paguridae) from an unique habitat. *Zootaxa*, 1116, 55–68.
- Milne-Edwards, A. (1880). Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, 78, 79, by the United States Coast Survey steamer "Blake", Lieut.-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. VIII. Études préliminaires sur les Crustacés. *Bulletin of the Museum of Comparative Zoology, Harvard College*, 8, 1–68.
- Milne-Edwards, A. & Bouvier, E.-L. (1893). Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78), in the Caribbean Sea (1878–79), and along the Atlantic coast of the United States (1880), by the U.S. Coast Survey Steamer "Blake", Lieut.-Commander C.D Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. XXXIII. Description des Crustacés de la famille des paguriens recueillis pendant l'expédition. *Memoirs of the Museum of Comparative Zoology, Harvard College*, 14(3), 5–172.
- Pilgrim, R.L.C. (1973). Axial skeleton and musculature in the thorax of the hermit crab, *Pagurus bernhardus* [Anomura: Paguridae]. *Journal of the Marine Biological Association United Kingdom*, 53, 363–396.
- Saint Laurent, M. de & McLaughlin, P.A. (2000). Superfamily Paguroidea, Family Paguridae. *In*: J. Forest, M. de Saint Laurent, P.A. McLaughlin, & R. Lemaitre, The marine fauna of New Zealand: Paguridea (Decapoda: Anomura) exclusive of the Lithodidae. *NIWA Biodiversity Memoir* 114, 104–209.
- Tudge, C.C. (1995). Ultrastructure and phylogeny of the spermatozoa of the infraorders Thalassinidea and Anomura (Decapoda, Crustacea). *In*: B.G.M. Jamieson, J. Ausio and J.-L Justine (eds.), Advances in spermatozoal phylogeny and taxonomy. *Mémoires du Museum national d'Histoire naturelle*, 166, 251–263.
- Tudge, C.C. & Jamieson, B.G.M. (1996). Spermatophore and spermatozoal morphology in the Porcellanidae. II. The genera *Petrolisthes* and *Polyonyx* (Decapoda: Anomura). *Journal of Crustacean Biology*, 16(3), 535–546.
- Türkay, M. (1986). Crustacea Decapoda Reptantia der Tiefsee des Roten Meeres. *Senckenbergiana Maritima*, 18(3/6), 123–185.
- Williams, J.D. & McDermott, J.J. (2004). Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates. *Journal of Experimental Marine Biology and Ecology*, 305, 11–128.